Concepts are Not “Webs of Sensation”: Evidence from motion words

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Abstract
What are concepts made of? One prominent theory assumes that concepts are comprised of sensory-motor features distributed throughout the sensory-motor cortices. For example, the meaning of the word “kick” is partially represented in the visual motion regions that are activated during the observation of kicking. This theory makes specific predictions about concepts that have motion properties: they are represented in motion perception regions. To test this prediction we used functional magnetic resonance imaging (fMRI) to localize brain regions involved in perception of motion and body movement. We investigated the response of these regions during word comprehension. Participants made relatedness judgments on word-pairs from several categories that varied in the degree to which they brought to mind visual motion (verbs of action, thought, change-of-state, and bodily-function; and nouns referring to animals, tools and inanimate natural kinds). The results show that none of the visual motion areas respond more to high-motion than low-motion words. We also tested the claim that concepts are not represented directly in sensory-motor cortices but in nearby regions. According to this version of this hypothesis, these brain regions store visual motion features that are retrieved during word comprehension. This theory predicts that posterior-lateral temporal cortices (PLTC) respond to action concepts because they represent motion associations. We replicated previous findings showing greater activity in the PLTC for action than animal concepts. These PLTC regions were observed just anterior to biological motion perception regions. Critically, regions that responded to action concepts did not respond more to high-motion than low-motion concepts. Rather, these regions responded more to all verbs than all nouns. We conclude that concepts are abstracted away from their associated sensory experiences.

Keywords: motion; concept; word; meaning; sensory-motor; amodal; modality-independent.

Introduction
What kinds of information are concepts comprised of and how is this information organized? According to ‘concept empiricism’ “All (human) concepts are copies or combinations of copies of perceptual representations” (Prinz, 2002, p. 18; Pulvermuller, 1999). Thus, concepts are said to be “webs of sensation” that are directly based in our sensory experiences. According to an alternative view, concepts are abstracted away from modality-specific experiences and are thus comprised of modality-independent representations. According to this view, concepts of events and entities are organized according to conceptual, rather than sensory-motor properties (Caramazza, Hillis, Rapp, & Romani, 1990; Rogers et al., 2004; Thompson-Schill, 2003; Thompson-Schill, Kan, & Oliver, 2006). These views on the role of sensory-motor experiences in shaping conceptual content shape current hypotheses of how concepts are instantiated in the brain. According to one view, concepts are represented in the sensory-motor cortices through which they were acquired (Pulvermuller, 1999, 2001). One source of support for this view comes from so called “motion words.” Action concepts, which possess motion associations, activate the posterior-lateral-temporal cortices (PLTC) (e.g. Damasio, Grabowski, Tranel, Hichwa, & et al., 1996; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995). This PLTC activation for action concepts is taken to reflect the retrieval of motion information, because several regions within the PLTC are involved in motion perception. Specifically, the middle temporal area (MT+) responds to most moving visual stimuli (Born & Bradley, 2005; Zeki, 1974). On the other hand, the right superior temporal sulcus (RSTS) is specifically important for biological motion perception (E. D. Grossman, Battelli, & Pascual-Leone, 2005). Based on the proximity of these motion perception regions to conceptual action regions in the PLTC it has been argued that action concepts consist in part of motion associations and are thus represented in motion perception regions.
Alternatively, the PLTC may contain modality independent representations of events or the grammatical types that typically refer to them i.e. verbs.

In the present study we directly addressed whether the PLTC stores representations of visual motion features or modality independent semantic or grammatical representations. We tested the hypothesis that action concepts partially represented in MT+ and/or the STS biological motion perception area. In two localizer experiments participants viewed simple motion and biological motion. Based on the localizer experiments, we identified area MT+ and the STS biological-motion-perception region bilaterally. In a third experiment, subjects performed a relatedness judgment task with word-pairs. We used various categories of words that varied systematically in their association with visual motion. (Motion associations were determined in a separate behavioral study.) We tested the prediction that visual motion perception regions respond selectively to words that are high in visual motion.

We also studied the nature of PLTC action representations. Do PLTC action regions respond preferentially to words with high motion features or to all event concepts, irrespective of their motion information? We answered this question by identifying previously described action concept regions in the PLTC and determining whether they responded to preferentially to high motion words, or to all verbs.

**Methods**

**Participants**

Twelve healthy native-English speakers (6 females) took part in the word comprehension experiment. The average age of the participants was 24 ($SD = 3$). Participants were all right-handed. All subjects gave informed consent and were paid $30 an hour for taking part in the experiment.

**Procedure**

Participants took part in three experiments during a single scan session. The first and main experiment was a word comprehension study. Additionally, there were two “localizer” experiments. In the Biological Motion Localizer Experiment we identified biological motion perception regions. In the Basic Motion Localizer Experiment we localized area MT+.

In the Word Comprehension Experiment, (five runs of 7 minutes and 42 seconds each) participants heard pairs of words and pronounceable non-words presented over headphones. For word trials, participants decided how related in meaning the two words were on a scale of one to four. For non-word trials, participants made a sound-similarity judgment. Participants responded to each pair by pressing buttons 1 through 4 on a respond pad. Word-pairs were presented in blocks of five and were blocked by condition. Blocks were 18 seconds long and were separated by 14 seconds of fixation. (fMRI and behavioral data for the non-word stimuli were not analyzed for the present study.)

Word stimuli consisted of: verbs of action, thought, change-of-state, and bodily-function; and nouns referring to animals, tools and inanimate natural kinds. Nouns and verbs were matched on familiarity and syllable length based on a prior rating study with a separate group of subjects (all $P's > .10$).

We obtained motion ratings for all words in a separate group of subjects (N=14). Participants rated words on the extent to which they led them to “imagine visual movement.” “That is, when you read or hear a word, do you see something moving in your mind's eye?”

In the Biological Motion Localizer Experiment, participants performed a one-back task with point-light animations of human actions such as walking and kicking (each once second long). The control condition consisted of scrambled point-light animations, which are perceived as meaningless dot movements rather than human actions (E. Grossman et al., 2000). The biological motion and control conditions were blocked, each block lasted 18 seconds and there was 12 second ITIs between blocks. The experiment consisted of two runs, 5 minutes and 10 seconds each.

During the Basic Motion Localizer Experiment, participants saw 4 types of blocks. Motion blocks consisted of the classic concentric ring task used to localize human area MT+. Concentric light and dark gray rings appeared to be moving outward or inward towards the center. In the motion control condition, the same concentric rings changed in luminance, but did not appear to be moving (see Tootell et al., 1995). (Pictures of bodies and artifacts were presented in the other two conditions.) Throughout the experiment, participants were instructed to fixate on the screen and were not required to make any responses.

**fMRI Data Acquisition and Analysis**

Structural and functional data were collected on a 3 Tesla Siemens scanner. Scanning was done at the Athinoula A. Martinos Imaging Center at the McGovern Institute for Brain Research at MIT. Structural images were collected with 2 mm isotropic voxels. Functional data were acquired in 3.12 x 3.13 x 4 mm voxels.

Data analysis was performed using SPM2 (SPM2 http://www.fil.ion.ucl.ac.uk/) and in-house software. The data were realigned, smoothed with a 5 mm smoothing kernel, and normalized to a standard template. The modified linear model was used to analyze BOLD activity of each subject as a function of condition, for each block. Covariates of interest were convolved with a standard hemodynamic response function (HRF). Nuisance covariates included: scan effects, an intercept term and the global signal covariate. Time series data were subjected to a high-pass low-pass filter.

Second level, whole-brain analyses were performed on the $\beta$-values obtained from the first-level models (False positive rate was controlled at $\alpha < .05$ (corrected) by performing Monte-Carlo permutation tests on the data).
Region of interest (ROI) analyses were performed on % signal change data relative to a rest baseline. Functional ROI’s were identified in individual subjects based on localizer experiments or orthogonal contrasts.

Results

Motion Rating Experiment

For the verbs, actions had the highest motion ratings, followed by change of state/bodily function verbs, and then by thought verbs. For the nouns, animals had the highest motion ratings, followed by tools, and then by natural kinds. Based on these ratings we defined groups of high and low motion words, collapsing across grammatical class.

Based on the collected ratings verbs and nouns were grouped into high, intermediate and low motion categories.

<table>
<thead>
<tr>
<th>Motion Group</th>
<th>Semantic Category</th>
<th>Motion Rating</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>Action</td>
<td>5.41 (.57)</td>
</tr>
<tr>
<td>Intermediate</td>
<td>Bodily and Change of State</td>
<td>3.30 (.92)</td>
</tr>
<tr>
<td>Low</td>
<td>Thought</td>
<td>2.42 (.68)</td>
</tr>
<tr>
<td>High</td>
<td>Animal</td>
<td>3.23 (.60)</td>
</tr>
<tr>
<td>Intermediate</td>
<td>Tool</td>
<td>2.81 (.55)</td>
</tr>
<tr>
<td>Low</td>
<td>Natural Kind</td>
<td>2.39 (.57)</td>
</tr>
</tbody>
</table>

Table 1. Motion categories.

For the fMRI analyses we created two motion contrasts. For contrast one, high-motion words included action verbs and animal nouns, whereas the low motion words included thought verbs and inanimate natural kind nouns. The high-motion words were reliably higher in motion ratings than low motion words ($t(13) = 7.73, P < .0001; t(198) = 13.84, P < .0001$) (Figure 1 A). In addition, we defined a secondary contrast of high and low motion words for comparison in regions that were identified by the action-verbs – animal nouns contrast (bodily function/change of state verbs + tool nouns – thought verbs – inanimate natural kind nouns).

These high and low motion sets were defined to be orthogonal to the action-verbs – animal nouns contrast and differed in motion ratings ($t(13) = 3.59, P < .01; t(198) = 6.48, P < .0001$).

Localizer Experiments

In the Biological Motion Localizer Experiment, the biological motion perception regions in the RSTS were identified in 11/11 subjects and the LSTS in 10/11 subjects. (Average peak voxels for the RSTS [58 -49 13] and LSTS [-57 -55 12] ) In the Basic Motion Localizer Experiment, right and left MT+ were localized in 11/11 subjects.

Word Comprehension Experiment

Participants judged the similarity of pairs of words. The average similarity was not different for nouns versus verbs ($M_{noun} = 1.86 \pm .38, M_{verb} = 1.85 \pm .34; t(8) = .28, P = .78$). Similarly, there was no difference in average similarity among categories of nouns (all $P’s > .3$). High motion words (action-verbs + animal nouns) did not differ in average pair-wise similarity from low motion words (thought verbs + inanimate natural kinds) ($t < 1, P < .3$).

Participants were significantly faster to respond to noun than verb-pairs ($M_{noun} = 1702 \pm 118$ msec, $M_{verb} = 1823 \pm 87$ msec; $t(8) = 5.06, P = .001$). High motion words did not differ in reaction time from low motion words ($t < 1, P < .3$). There were no differences in reaction time among categories of nouns or verbs (all $P’s > .3$).

Do motion perception regions distinguish between motion and non-motion words?

To answer this question, we examined activity during word comprehension in bilateral MT+ and STS. In each region, we tested whether the response differentiated between the two highest motion word categories (Action Verbs + Animal Nouns) and the two lowest motion word categories.
(Thought Verbs + Natural Nouns). We also assessed whether any of these regions differentiated among grammatical classes (verbs vs. nouns).

Percent signal change did not differ among word types within the right or the left MT+ ROIs: high motion words did not differ from low-motion words, nor did verbs differ from nouns. No verb and noun types differed from each other (F < 2, P > .2). In fact, the BOLD response in left and right MT+ was reliably lower, during all word conditions, than during rest (M_{MT} = -.35 ± .24, t(10) = -4.92, P < .0001; M_{RT} = -.36 ± .24, t(10) = -4.96, P < .0001).

In the RSTS, high motion words did not differ from low motion words, nor did verbs differ from nouns (t < 1, P > .3). None of the verb and noun categories differ amongst themselves (F < 1, P > .3). Activity in the RSTS was not different from rest during word comprehension (M = .01 ± .20, t(10) = -.12, P = .88). In the LSTS, BOLD signal did not differ from fixation (M = .11 ± .34, t = 1, P = .3). High motion words did not differ from low motion words (t < 1, P > .25). However, verbs produced greater activity than nouns (M_verb = .18 ± .44, M_noun = .03 ± .24, t(10) = 3.53, P < .001). This effect remained reliable when reaction time was included as a covariate in each subject’s model (t(7) = 2.79, P < .05). None of the verb categories differed among themselves (F < 1, P > .3). Among the nouns, natural objects produced greater activity than animals (F(2,11) = 6.4, P < .01, Tukey HSD Q = 2.53, P < .05). (See Figure 1 B for summary of the results.)

**Do regions that respond to action concept in the PLTC respond preferentially to words with high motion associations?**

Replicating previous results, we found greater activity for action-verbs than names of animals in the PLTC (The whole-brain left PLTC effect remained reliable when RT was included as a covariate in the model.) We examined whether this effect was due to the greater motion content of action-verbs. Action > Animal regions were defined in individual subjects within the right and left PLTC. In the left PLTC there was a superior region close to the temporoparietal junction (LTPJ) (average peak -58 -48 22) and an inferior region on the STS (-57 -41 -1). In the right hemisphere we identified one region on the STS (10/12 subjects; 57 -46 11). The motion hypothesis predicts these regions should show a higher response to the names of tools and bodily function/change of state verbs (higher motion) than to the names of natural kinds and thought verbs (lower motion; this contrast defined the “motion effect” orthogonal to the Animal Noun – Action Verb contrast).

Alternatively, we hypothesized that these regions might differentiate between Action Verbs and Animals Nouns based on a property related to grammatical class, but independent of associations with motion. We therefore defined an alternative prediction, using the same four word categories (grammatical class effect: bodily function/change of state verbs and thought verbs more than names of natural objects and tools). These grammatical class groupings did not differ in average motion ratings in the prior behavioral experiment (t(13) < 1, P > .3).

None of the left or right PLTC action-verb regions showed a motion effect (see Figure 1 B, t < 1, P > .5). In contrast, both of the left PLTC regions showed greater activity for verbs than nouns (t > 5, P < .0001). The difference between verbs and nouns in the LPLTC regions remained reliable after RT was included as a covariate in the model (LSTS t(7) = 3.60, P < .01; LTPJ t(7) = 7.28, P < .0001). The RSTS region showed a trend for greater activity for verbs (t(9) = 1.78, P < .1).

Because many of the regions identified as differentiated Actions > Animals, and one region involved in motion perception, appeared to primarily be differentiating words based on their grammatical class, we further investigated PLTC brain regions in which there was a greater response to verbs than nouns. We used two analysis strategies. First we used the contrast Verbs > Nouns to identify new regions of interest, and tested whether any of these regions differentiated between word categories based on motion associations. Second, we examined whether any of the regions that differentiate between Verbs and Nouns overlap, even partly, with brain regions involved in the perception of motion or biological motion.

Three regions that responded more to verbs than nouns were identified in the right and left PLTC respectively. In these regions, we compared the highest motion categories to the lowest motion categories (action-verbs + animals – thought verbs – natural kinds). None of the verb selective regions examined showed a motion effect (t’s < 1, P > .3).

We then examined whether regions involved in motion perception overlap with verb-selective regions in whole-brain analysis. There was no overlap between regions involved in basic motion perception (Motion vs No-motion, Localizer), and regions that differentiated between nouns and verbs. On the other hand, in the group-average, one region of overlap was observed for verb comprehension and biological motion perception in the right PLTC (Verb > Nouns and Biological Motion > Scrambled Motion). Since group averaging leads to spatial blurring of nearby activations, we investigated the overlap between verb comprehension and biological motion perception in individual subjects. We calculated the percent of all voxels active for both verb comprehension and biological motion perception (relative to the total number of voxel active in both tasks) (see methods for details). On average in the right posterior temporal lobe 3.1 ± 3.4% (range 0% to 11%) of voxels overlapped between verb comprehension and biological motion perception. In the left PLTC we observed 4.4 ± 6.8% overlap (range 0% to 22%).

We looked for motion effects (high-motion over low-motion words) in those voxels that overlapped between verb comprehension and biological motion perception in each subject. Motion and non-motion words did not differ in the overlap regions (t(8) < 1, P > .3).
Finally, the whole brain analyses did not reveal any regions that were more active for motion than non-motion words.

**Discussion**

Numerous studies have reported a greater neural response in the PLTC to actions than other categories of concepts, as well as other stimuli such as non-words and false fonts (e.g. Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Martin, Wiggs, Ungerleider, & Haxby, 1996). These data were attributed to the greater motion information associated with action concepts relative to other categories. According to this interpretation, regions in the PLTC that support motion perception also represent concepts that have motion associations. As such, these data have been taken to support a sensory-motor account of concept representation. Contrary to these claims, we demonstrate that motion perception regions do not respond to the motion associations of these concepts during word comprehension.

We also tested a weaker claim of eliminative SMH that conceptual action regions in the PLTC respond selectively to words with high motion associations. We identified action concepts regions by replicating previous findings showing greater activity for action-verbs than nouns referring to animals. However, we found that these brain regions do not selectively respond to concepts with high motion associations. The PLTC regions that respond to action-verbs, respond more to all verbs than all nouns, irrespective of whether these have motion associations. In fact, no PLTC region showed greater activity for motion words than non-motion words in whole-brain or any of the ROI analyses. Rather, we observed several regions in the PLTC that responded more to all verbs than all nouns. These data illustrate that presence or absence of motion information is not a dimension along which concepts are organized in the PLTC. Thus, PLTC action concept regions do not contain copies of sensory features.

In the present study, participants performed a semantic task with words that have motion associations, without activating motion perception cortices, or activating any brain regions that respond selectively to the presence of visual motion. These data illustrate that retrieving sensory-motor features is not necessary for word comprehension.

Our data demonstrate that contrary to the claim of eliminative SMH, concepts are not exclusively comprised of sensory-motor features. However, they do not preclude the possibility that sensory-motor features play a role in conceptual thought (Caramazza & Mahon, 2003; Machery, 2006, 2007; Oliver & Thompson-Schill, 2003; Rogers et al., 2004; Tyler & Moss, 2001; Tyler et al., 2003). In the present experiment, we did not require subjects to specifically attend to, or imagine, the motion features of words. Given such instructions, it is possible we would have observed activity in motion perception regions. However, simply making the visual motion features of words pertinent to semantic decisions, is not sufficient to activate area MT+ (Kable et al., 2005). An interesting question for future research concerns the circumstances during natural language comprehension that lead to the retrieval of sensory-motor information and the role that activation of such features might play in behavior.

Although we found that motion perception regions do not represent motion aspects of action concepts, we found that at least some of the PLTC verb-selective regions are just anterior to biological motion perception regions. Previous studies have shown that the right and left PLTC shows greater activity for verbs than nouns (e.g. Bedny & Thompson-Schill, 2006; Davis, Meunier, & Marslen-Wilson, 2004). We found that the vast majority of verb comprehension cortex and biological motion perception cortex in the PLTC are non-overlapping. However, there was a small amount of overlap (less than 5%) between biological motion perception and verb selective cortices in the PLTC. This overlap may reflect true functional overlap. Alternatively, verb comprehension and biological motion perception may be separable above the resolution of the current study. However, at the very least our results indicate that if not overlapping, PLTC verb regions are systematically near biological motion perception regions.

This finding is consistent with a version of the anterior shift hypothesis proposed by Thompson-Schill and colleagues (Kable et al., 2005; Thompson-Schill, 2003; Thompson-Schill et al., 2006). According to this hypothesis, semantic regions lie anterior to perceptual regions that are important for acquiring information about a particular category of concepts. However, information in these anterior semantic regions may be organized along entirely different dimensions than in the posterior sensory regions. Consistent with this claim, we find that regions anterior to biological perception regions respond selectively to verbs, irrespective of motion content. What might verbs and biological motion have to do with each other? Verbs tend to refer to events, rather than entities (which are usually referred to by nouns). It is possible that during development, motion is in an important source of information for learning about events. And thus events come to be represented in the PLTC because of the input they receive from biological motion perception regions during ontogeny. Alternatively, the anterior shift from biological motion perception to verbs could have occurred through evolution. That is, there may be an evolutionary relationship between motion perception and event representations. We note that these interpretations of the data are at present speculative. The proximity of biological motion perception and verb regions may be coincidental. Future research is required to resolve this question.

**Conclusions**

Our data demonstrate that visual motion features are not activated when we comprehend words that have visual motion associations. Motion perception regions do not respond preferentially to words with motion associations during word comprehension. Furthermore, PLTC regions that respond to action concepts do not respond preferentially to words with motion associations. Rather, these regions...
respond preferentially to all verbs than all nouns. These data illustrate that word comprehension can and does occur without the activation of sensory associations. Therefore, if the concept of “concept” is to explain basic linguistic behavior, there must be more to concepts than sensory-motor features.

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